

A critical examination of indices of dynamic interaction for wildlife telemetry studies

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Running Head: indices of dynamic interaction

Summary / Abstract

1. Wildlife scientists continue to be interested in studying ways to quantify how the movements of animals are inter-dependent – *dynamic interaction*. While a number of applied studies of dynamic interaction exist, little is known about the comparative effectiveness and applicability of available methods used for quantifying interactions among animals.
2. We highlight the formulation, implementation, and interpretation of a suite of eight currently available indices of dynamic interaction. Point- and path-based approaches are contrasted to demonstrate differences between methods and underlying assumptions on telemetry data.
3. Correlated and biased-correlated random walks were simulated at a range of sampling resolutions to generate scenarios with dynamic interaction present and absent. We evaluate the effectiveness of each index at identifying differing types of interactive behaviour at each sampling resolution. Each index is then applied to an empirical telemetry dataset of three white-tailed deer (*Odocoileus virginianus*) dyads.
4. Results from the simulated data show that three indices of dynamic interaction reliant on statistical testing procedures are susceptible to Type I error, which increases at fine sampling resolutions. In the white-tailed deer examples, a recently developed index for quantifying local-level cohesive movement behaviour (the di index) provides revealing information on the presence of infrequent and varying interactions in space and time.
5. Point-based approaches implemented with finely sampled telemetry data over-estimate the presence of interactions (Type I errors). Indices producing only a single global statistic (7 of the 8 indices) are unable to quantify infrequent and varying interactions

through time. The quantification of infrequent and variable interactive behaviour has important implications for the spread of disease, and the prevalence of social behaviour in wildlife. Guidelines are presented to inform researchers wishing to study dynamic interaction patterns in their own telemetry datasets. Finally, we make openly available our code, in the statistical software R, for computing each index of dynamic interaction presented herein.

Keywords: contact rate, static interaction, proximity, simulation, biased random walk, sampling resolution, *Odocoileus virginianus*, GPS telemetry

1 – Introduction

The development of GPS tracking technologies is revolutionizing wildlife movement and behaviour research (Cagnacci *et al.* 2010), and has led to increased interest in the study of interactions among individual animals (e.g., mating behaviour, Stenhouse *et al.* 2005; and predator-prey dynamics, Eriksen *et al.* 2008). Interactive behaviour can be characterized as either static or dynamic (Macdonald, Ball & Hough 1980). Static interaction can be defined simply as the joint-space use between two individuals, ignoring the temporal information of location fixes, (Kernohan, Gitzen & Millspaugh 2001), and is typically measured by an index of home range overlap or volume of intersection using utilization distributions (Millspaugh *et al.* 2004; Fieberg & Kochanny 2005). Alternatively, dynamic interaction refers to how the movements of two individuals are related (Macdonald *et al.* 1980), or as the inter-dependency in the movement of two individuals (Doncaster 1990). Strictly speaking, the presence of dynamic interaction implies some degree of static interaction, while the converse may or may not be true. Tests for dynamic interaction can be used to examine attraction or avoidance behaviour (Doncaster 1990), simultaneous joint-space use (Minta, 1992), or cohesiveness in the movements of two individuals (Long & Nelson 2013). A number of techniques for studying dynamic interactions have been developed and adopted widely in wildlife telemetry studies (see Table 1), but little is known about the effectiveness of each at identifying true dynamic interaction patterns. Similarly, it is difficult for researchers to compare results among existing methods because most applied studies typically implement only a single method.

< Approximate location of Table 1 >

Novel tracking technologies (e.g., GPS, Argos, Platform terminal transmitters (PTTs), global satellite Iridium systems, etc.) are changing the manner in which wildlife telemetry data

are recorded and transmitted. A wide variety of systems can be programmed to collect telemetry fixes at variable sampling resolutions (Tomkiewicz *et al.* 2010). Sampling resolutions (the frequency at which telemetry fixes are collected) previously unattainable are now routinely implemented in modern tracking studies. However, many studies still employ coarser resolution telemetry systems (e.g., VHF telemetry), which have a lower unit cost in order to monitor a greater number of individuals (Girard *et al.* 2006). In addition to the wide range of technologies, study objectives typically dictate sample size, sampling resolution, and study design, all of which may influence the ways in which data are analyzed and interpreted. Therefore, researchers are often left with the difficult task of identifying which, of a suite of available analytical techniques, are appropriate for meeting study objectives.

The overall goal of this study is to demonstrate the effectiveness of eight available indices for measuring dynamic interaction common to wildlife telemetry data using both simulated and empirical data. Our objectives were to: 1) review the formulation and interpretation of each of the eight indices, 2) detect present vs. absent dynamic interaction using simulated data at varying sampling resolutions, 3) evaluate each method using empirical data collected on white-tailed deer fitted with GPS collars, 4) highlight the advantages and disadvantages of each approach, and 5) provide guidance on the selection, use, and interpretation of dynamic interaction indices common to analysis of wildlife telemetry data. Areas of future research are discussed to encourage the development of additional tools and algorithms that can be used in association with dynamic interaction analysis. Last, we provide code for the R statistical computing environment that allows researchers to implement each of the eight indices of dynamic interaction presented herein.

2 – Indices of Dynamic Interaction

Indices of dynamic interaction can be broadly categorized as point-based or path-based, depending on how they represent telemetry data (as points, or as connected segments – paths). Clear conceptual differences in the calculation and interpretation of the eight dynamic indices are apparent from their individual formulation (see below and Table 2), but also between point- and path-based approaches. Point-based indices typically examine attraction/avoidance behaviour, while path-based indices look at cohesive movement behaviour. Of the eight currently available indices of dynamic interaction, six are point-based, while two are path-based (Table 2). The terminology and notation used for describing telemetry data and concepts relating to measurement of dynamic interaction is introduced in Table 3.

< Approximate location Table 2 >

< Approximate location Table 3 >

2.1 – Proximity analysis

Dynamic interaction is most simply quantified as a measure of nearness in space. Researchers have used proximity analysis (Prox) to understand the frequency at which two individuals are near each other. The simplest such index is the proximity rate:

$$\text{Prox} = \frac{ST_{\alpha\beta}}{T_{\alpha\beta}}$$

where Prox measures the proportion of simultaneous fixes ($T_{\alpha\beta}$ – defined using temporal threshold – t_c) that are spatially proximal ($ST_{\alpha\beta}$ – based on spatial threshold d_c). The value of implementing Prox is that it is easily interpreted and gives an estimate of the proportion of time animals are proximal in space (within d_c distance units), given the fixes that are close in time (based on temporal threshold t_c) (Table 2). Further analysis can examine temporally the binary sequence of proximal and non-proximal fixes. Prox has been used as an indicator of attraction between individuals (e.g., Bertrand *et al.* 1996), and as an estimate of contact rates, which is

useful when studying disease spread dynamics (Baker & Harris 2000). The requirement of a distance threshold is both advantageous and problematic. In some cases, such as with contact rates, a biologically motivated spatial distance may be used. However, in many cases, it will be chosen subjectively by the researcher, owing to previously used thresholds in the literature, or some other property of the data such as error or sampling interval. In these cases, the subjectivity of the chosen threshold will impact the results as various choices for d_c will change Prox results.

2.2 – Coefficient of association

The coefficient of association (Ca) was first introduced by Cole (1949) for measuring interspecific associations in field samples and has since been identified as a potential measure of dynamic interaction in wildlife telemetry data (Bauman 1998). Coefficient of association is calculated as:

$$Ca = \frac{2 ST_{\alpha\beta}}{n_{\alpha} + n_{\beta}}$$

where n_{α} (resp. n_{β}) is the total number of all fixes in α (resp. β). Ca is similar to Prox, only Ca measures the rate of all fixes that are $ST_{\alpha\beta}$, not just the simultaneous fixes; thus Ca is measuring the same phenomenon as Prox. Typically, $Ca > 0.5$ indicates attraction, while $Ca < 0.5$ indicates no association (Kernohan *et al.* 2001; Table 2). Like Prox, Ca is a useful indicator of attraction and contact rates, as defined by the threshold d_c . However, it is similarly affected by the subjectivity with which d_c is determined.

2.3 – Coefficient of sociality

The coefficient of sociality (Cs) was proposed by Kenward *et al.* (1993) as an alternative measure of attraction using the raw distances between fixes, rather than a user-defined threshold. The formulation of Cs is a variant of Jacobs' index (Jacobs 1974), a metric originally proposed for measuring food selection by wildlife. Cs is calculated as:

$$C_s = \frac{d_E - d_o}{d_E + d_o}$$

where d_o is the mean spatial distance between $T_{\alpha\beta}$ fixes and d_E is the expected mean distance, based on n^2 permutations of the $T_{\alpha\beta}$ fixes. The statistic is symmetric (on [-1, 1]) where positive values suggest attraction while negative values suggest avoidance. A Wilcoxon signed-rank test can be used to examine the significance of the resulting C_s value (Table 2). A major limitation is determining a reasonable expectation of mean distance to test against. Generally, the distribution of distances of the n^2 permutations of all $T_{\alpha\beta}$ telemetry fixes is used to determine d_E . Others have suggested that d_E can be determined via simulations using, for example, correlated random walks (Miller 2012).

2.4 – Doncaster's non-parametric test

Doncaster (1990) proposed a non-parametric test for interaction (Don) by examining the separations between the n $T_{\alpha\beta}$ fixes and the unpaired $n^2 - n$ permutations of the $T_{\alpha\beta}$ fixes, and is analogous to the Knox test for space-time clustering (Knox 1964). The cumulative distribution of the $T_{\alpha\beta}$ fix distances can be compared graphically with the cumulative distribution of the $n^2 - n$ permuted distances. For example, Don is useful for determining a suitable distance threshold (d_c) by identifying where the $T_{\alpha\beta}$ plot is above the expected line based on the permutations. Upon selecting a suitable d_c value, a contingency table can be constructed, identifying the number of $T_{\alpha\beta}$ and non- $T_{\alpha\beta}$ (termed 'unpaired') fix distances that are above and below the threshold d_c . A χ^2 test (with 1 d.f.) or a binomial test can be used to examine the statistical significance of the counts of $T_{\alpha\beta}$ and non- $T_{\alpha\beta}$ distances above and below d_c (Table 2). A modified version of Don replaces the expectations derived from the $n^2 - n$ permutations of the $T_{\alpha\beta}$ fixes with a simulation procedure based on correlated random walks (White & Harris 1994).

2.5 – Minta's test for spatial and temporal interaction

Minta (1992) introduced three statistics (L_{AA} , L_{BB} , and L_{ixn}) for examining the spatial and temporal interactions between two individuals. L_{AA} and L_{BB} ignore the temporal information from fixes and represent only spatial measures of interaction. Here, we focus on L_{ixn} , which is a statistic for examining temporal interaction. L_{ixn} requires the calculation of individual home ranges, typically from the collected telemetry data, which are then divided (using a spatial intersection) into three areas: 1) used by α only, 2) used by β only, and 3) shared by α and β (often termed the overlap zone; see Table 1 for notations). The number of fixes contained in each area (i.e., used by α only, used by β only, and the shared area) are tested against expectations representing the probability of finding the animal in each of these areas. Expectation probabilities can be derived by using either the proportions of all fixes contained in each area, or the overlap area percentages (see Minta 1992). In the case of overlap area percentages, it is assumed the relative areas associated with space used by α only, by β only, and the shared area, are proportional to the amount of use.

The L_{ixn} statistic is a function of the ratio of simultaneous use and avoidance of the shared area to that of the solitary use of the shared area, and is calculated by:

$$L_{ixn} = \log \left| \frac{\left(\frac{n_{\alpha\beta}}{p_{\alpha\beta}} + \frac{n_{00}}{p_{00}} \right)}{\left(\frac{n_{\alpha 0}}{p_{\alpha 0}} + \frac{n_{0\beta}}{p_{0\beta}} \right)} \right|$$

where n represents the number of observed fixes, p is the expectation probability, and the subscripts α and β signify each individual's presence in the shared area, while the subscript 0 signifies absence from the shared area. Thus, L_{ixn} measures the simultaneous use (defined using temporal threshold t_c) of the shared area. Positive L_{ixn} values suggest simultaneous use of the shared area (attraction), while negative values indicate solitary use of the shared area

(avoidance). Lixn near 0 indicates indifference or random use of the shared area. The Lixn statistic can be tested for significance using a χ^2 test with 1 df from the contingency table of observed and expected frequencies of use within the shared area (Table 2).

2.6 – Half-weight association index

The half-weight association index (HAI - Brotherton *et al.* 1997) represents a companion test to the Minta (1992) Lixn temporal interaction statistic (Atwood & Weeks 2003). As in Lixn, HAI is based on the shared area between the two individual home ranges (the overlap zone). The HAI statistic is however a more localized approach, focusing only on those fixes contained in the shared area (or only on the area of static interaction). HAI is calculated as:

$$HAI = \frac{ST_{\alpha\beta}}{ST_{\alpha\beta} + \frac{(x + y)}{2}}$$

where x and y are the number of solitary fixes (for α and β , respectively) within the shared area. Values near 1 indicate attraction (within the shared area) and values near 0 indicate avoidance (within the shared area; Table 2). HAI is computed identically to Ca , but only for those fixes contained in the shared area of the home range. Thus, for a dyad consisting of two individuals with identical home ranges, $Ca = HAI$.

2.7 – Correlation index

Shirabe (2006) introduced a correlation index (Cr) for analyzing movement data, which can be considered a type of path-based measure of dynamic interaction. The Cr index takes the form of a Pearson product-moment correlation statistic for multivariate data (in this case bivariate in the two spatial dimensions, X and Y). With Cr, movement data are represented as time-series with vectors corresponding to movement segments that connect consecutive fixes (see Table 3). Cr

measures differences in corresponding vectors with respect to overall path means to determine the correlation structure of the data. Cr is calculated as:

$$Cr = \frac{\sum_{t=1}^{n-1} (v_t - \bar{v}) \cdot (w_t - \bar{w})}{\sqrt{\sum_{t=1}^{n-1} |v_t - \bar{v}|^2} \sqrt{\sum_{t=1}^{n-1} |w_t - \bar{w}|^2}}$$

where v_t and w_t represent movement vectors (for α and β) corresponding to time t , and \bar{v} and \bar{w} are mean vectors. Cr is interpreted similarly to other correlation statistics; values range from -1 to 1 where positive values indicate stronger correlation (cohesive movement), negative values indicate negative correlation (opposing movement), and values near 0 indicate random movement with respect to the other individual (Table 2). The mean vectors (\bar{v} and \bar{w}) represent the average speed and direction of travel of an object, which may or may not have relevance in the context of measuring and interpreting the presence of dynamic interactions, but strongly influence the results from Cr.

2.8 – Dynamic interaction index

Recently, Long & Nelson (2013) introduced a dynamic interaction index (DI) based on path-based methods, similar to earlier attempts of Shirabe (2006). The DI index attempts to measure the cohesiveness of corresponding movement vectors. DI is constructed as the mean of a localized version (termed di). Here, di is calculated as

$$di = \left(1 - \frac{|d_t^\alpha - d_t^\beta|}{d_t^\alpha + d_t^\beta} \right) \times \cos(\theta_t^\alpha - \theta_t^\beta) \text{ whereas DI is calculated by}$$

$$DI = \frac{1}{n-1} \sum_{i=1}^{n-1} di$$

where d is displacement and θ (the direction) of vector t for individual α or β . The localized di is simply the product of terms measuring cohesiveness in displacement and direction for each

corresponding segment. Thus, d_i is capable of separately measuring cohesiveness in the distance and direction components (d_{i_d} and d_{i_θ} respectively), which can be averaged into global statistics (see Long & Nelson 2013 for more details). Temporal trends in d_i can be used to identify periods of cohesive, opposing, and random movement within a dyad. The DI approach, as in Cr, measures cohesiveness irrespective of proximity between corresponding movement vectors (Table 2). Thus, to justify DI analysis, the researcher is required to have some *a priori* expectation of cohesive movement, which for example, can be based on proximity (defined by distance threshold d_c), a measure of static interaction (e.g., home range overlap), or simultaneous capture (e.g., familial groups). DI can then be set to 0 when these conditions are not met.

3 – Testing Indices

3.1 – Simulated Data

In order to test methods of dynamic interaction, we simulated situations where dynamic interaction would be present vs. absent. Generating movement dyads without dynamic interaction can be accomplished by simulating two independent correlated random walks (CRW) (White & Harris 1994; Miller 2012). When we simulated the absence of dynamic interaction, the origin of the second independent CRW was chosen to be a random location within the bounding box of the first CRW to offer the potential for static interaction (see Figure 1a). CRW's are governed by two parameters – h and r . The step-length parameter ($h > 0$) controls movement distances, and represents a multiplicative value for random draws from a step-length distribution (e.g., $l = h \times d$, d a random draw from a step-length distribution). The turning correlation parameter (r) governs the amount of correlation in turning direction, which is interpreted simply as a sliding scale from $r = 0$ (no correlation) to $r = 1$ (complete correlation in turning direction). Turning angles then were drawn from a circular distribution with $\mu = 0$, and $\sigma = f(r)$. Here we

use `simm.crw` function in the `adehabitatLT` package in R (Calenge 2006), which employs the chi distribution for step-lengths and a wrapped normal distribution for turning direction. In our simulations, h was varied across the range 1 – 5, and r between 0 and 0.5 to produce a range of scenarios with low to moderate amounts of correlation.

Unfortunately, no studies have simulated the presence of dynamic interaction in wildlife dyads. Therefore, we use the following procedure for simulating trajectories where dynamic interaction is present. Two trajectories are simultaneously generated, the first a CRW (as in the absent scenario), the second a random walk consisting of combinations (McClintock *et al.* 2012) of CRW and biased correlated random walks (BCRW; Barton *et al.* 2009). To emulate interactive behaviour, we modeled the bias towards the current position of the first CRW (i.e., the movement direction of the BCRW at time t is towards the position of the first CRW at time $t+1$). If we had biased the CRW throughout the entire second simulated trajectory, it would have produced a strong level of dynamic interaction at all times, which is unrealistic for many wildlife scenarios. A more realistic scenario is one where behaviour may shift between interactive and non-interactive phases. In the second trajectory, we simulate behaviour switches from non-interactive into interactive phases (CRW to BCRW and vice-versa) with transition probability p , resulting in varied amounts of time spent in the interactive phase. The range of values chosen for p ($0.001 \leq p \leq 0.005$) was appropriate for producing a realistic behaviour in our simulations given that we simulated trajectories with $n = 2000$ to 3000 fixes. During the interactive phase, step-lengths of the second trajectory were constrained so that the difference in step-lengths between the first and second trajectories was $\leq 25\%$, producing realistic patterns of interaction in movement speed as well as movement direction.

In a BCRW, three parameters (b , c , and ρ) govern different aspects of the bias effect (Barton *et al.* 2009). We randomly varied the bias strength parameter (b) across a range of acceptable values ($0.5 \leq b \leq 4$; Barton *et al.* 2009; Fronhofer, Hovestadt & Poethke 2013). The shape parameter (c) governs how the proximity of the two individuals influences the magnitude of the bias, which was varied randomly across a range of realistic values ($-0.3 \leq c \leq 0.3$). Finally, ρ is a correlation parameter for the turning distribution, similar to r from the CRW, which we also varied following previous studies ($0.8 \leq \rho \leq 0.9$; Barton *et al.* 2009; Fronhofer *et al.* 2013). For more information see the Supplementary Material which contains the R code used for simulating the presence of interaction with the BCRW, alongside a figure that demonstrates a dyad with interaction present and a dyad with interaction absent. In total, 1000 simulated scenarios were created to serve as a testing dataset, each containing two simulated dyads, one with dynamic interaction present and one with dynamic interaction absent.

In order to examine the effect of varying sampling resolutions on indices of dynamic interaction, we systematically down-sampled the simulated trajectories representing high resolution telemetry data at four coarser levels (50%, 33%, 20%, and 10% of the original fixes). This resulted in 1000 scenarios at each of five sampling resolutions (i.e., 100%, 50%, 33%, 20%, and 10% of original fixes), each containing one dyad with dynamic interaction absent, and one with dynamic interaction present.

3.2 – Empirical Data: White-tailed Deer GPS Telemetry Data

We collected data on a number of white-tailed deer from two study areas in south-central Oklahoma, USA. Study site 1 was 1,214 ha in size, and was surrounded by a 15-strand, high-tensile electric fence, thus restricting movement across property boundaries (2.5-m tall; Webb *et al.* 2009). Study site 2 was 1,861 ha and consisted of 5-strand barbed-wire fences, which

allowed deer to cross property boundaries unrestricted. Vegetation on both study sites was consistent with that of the Cross Timbers and Prairies ecoregion (Gee *et al.* 1994). On both study sites, we captured deer during January–March (1998–2005 on study site 1; 2010–2012 on study site 2) using modified drop-net systems (Gee, Holman & Demarais 1999). We sedated deer using intramuscular injections of telazol (4.4 mg/kg) and xylazine (2.2 mg/kg), and used yohimbine as an antagonist at 0.125 mg/kg. We fitted deer with GPS collars (ATS G2000 remote-release collars; Advanced Telemetry Systems, Inc., Isanti, MN) programmed to collected 1 fix every 15 (study site 1) or 30 minutes (study site 2). On study site 1, collars were capable of collecting data for ~3 months, and on study site 2, collars collected data for ~6 months. All capture, handling, and marking procedures were consistent with the guidelines of the American Society of Mammalogists (Gannon *et al.* 2007) and were approved by permit from the Oklahoma Department of Wildlife Conservation.

Three dyads of white-tailed deer (dyad 1 and 3 from study site 1 and dyad 2 from study site 2) were selected to further demonstrate the performance of each index of dynamic interaction using empirical telemetry data. We began with high-resolution GPS data recorded at a 30 min sampling resolution¹, but systematically resampled data to reflect coarser fix intervals (i.e., 6 and 24 hours); which is a common practice (Webb *et al.* 2010). Final evaluation of dynamic interaction measures occurred at three sampling resolutions: 30 min, 6 hour, and 24 hours.

We delineated 95% volume contour home ranges using the kernel density estimate (Worton 1989) and the *ad hoc* bandwidth, which assumes the resulting density surface is bivariate normal (Silverman 1986). For each dyad, we calculated the area of overlap of the two home ranges (interpreted as the proportion of home range overlap - AOP; Millspaugh *et al.*

¹ Dyads 1 and 3 were tracked using a 15 min sampling resolution, but here we resampled the temporal resolution to 30 min for consistency with dyad 2.

2004) as a measure of static interaction that can be used as an *a priori* indicator of the potential for dynamic interaction in dyads. Similar to other studies, our hypothesis on the presence of dynamic interaction behaviour is based on a hierarchical approach where we first examine static interaction (home range overlap) between individuals (Figure 1), and subsequently look at finer resolution dynamic interactions. We predict little dynamic interaction in dyad 1 (AOP = 0.17), but greater dynamic interaction in dyads 2 and 3 (AOP = 0.67 and 0.57, respectively). We test these *a priori* predictions at all three sampling resolutions.

< Approximate location Figure 1 >

3.3 – Calculating measures of dynamic interaction

All eight indices of dynamic interaction (Table 2) were computed for each of the dyads in the simulation study and using empirical GPS data from white-tailed deer. Several of the indices required the selection of parameter thresholds for identifying $T_{\alpha\beta}$ fixes and $S_{\alpha\beta}$ fixes. A t_c threshold of $\frac{1}{2}$ the sampling resolution was used to determine simultaneous fixes, for example $t_c = 15$ min was used with the 30 min white tailed deer telemetry data. In the simulation study, a distance threshold parameter of $d_c = 2 * h$ was used, where h is the step-length parameter in the CRW. Previous research on deer interactions has used $d_c = 24$ m (Bertrand *et al.* 1996). We selected a more conservative value of $d_c = 50$ m based on visual observations of deer and because there would be greater potential for identifying dynamic interactions at this spatial resolution for testing purposes. However, depending on specific hypotheses to test, the spatial threshold may be adjusted higher or lower, and comparison across spatial thresholds could help identify the scale at which processes are occurring across the landscape. Validating identified thresholds for d_c using independent dyads will provide evidence as to whether a given threshold is appropriate.

We evaluate results of the 1000 simulations, examining the mean and standard deviation of results from each index, for both the present and absent scenarios, along with significance of statistical tests where appropriate. Histograms of index values for both the present and absent scenarios are shown to highlight the distribution of results. Where statistical tests are employed (i.e., in Don, Lixn, and Cs), we use an α -level of 0.01 to identify significant values. Results are used to explore the effect of sampling resolution on each dynamic interaction index and to compare among the various indices for measuring dynamic interaction in telemetry studies. The relationship between index values and the amount of time spent in the interactive phase (in those dyads with interaction simulated as present) is investigated using scatterplots and correlation coefficients to quantify the effectiveness of indices for characterizing interactive behaviour, and to identify scenarios where misleading results may occur. In those dyads where no interaction was simulated (absent scenarios), the relationship between index values is compared to the level of static interaction (AOP) in the dyad to discover how the level of static interaction influences misleading inferences when interaction is absent. We chose one pair of dyads (see the Supplementary Material) to examine in finer detail the performance of each index in scenarios where interaction is present or absent. We compute index values at each resolution, along with time-series plots to demonstrate how local analysis facilitates a finer treatment of interactive behaviour.

In the white-tailed deer examples, we examine each index in finer detail for each individual dyad. We explore the use of the local di statistic (Sec. 2.8) to examine temporal variations in dynamic interaction behavior in these three dyads. At the finest sampling interval (such as the 30 min sampling resolution here), the time-series plots of di can be noisy, making

interpretation of patterns difficult. To circumvent this problem, we present the time-series plot of di for the 30 min data using a 24 hour moving average.

4 – Results

4.1 Simulated Data

Using simulated data to generate scenarios where dynamic interaction is present and absent provided a useful means for assessing the differences and similarities between the eight indices of dynamic interaction. Histograms for Prox, Ca, and HAI reveal that these three indices are each capable of identifying cases where dynamic interaction was present and absent (Figure 2). All three indices are comparable in terms of interpretation, but the Prox and Ca indices are essentially identical. The Prox, Ca, and HAI indices all appear to be robust to changes in sampling resolution (Figure 2). The Don statistic also performed well, identifying interaction (i.e., attraction) in all 1000 of the present scenarios, at each sampling resolution (Figure 2). However, at all sampling resolutions, Don produced unexpectedly high Type I error; for example, given that an α -level of 0.01 was used in the Don test, the number of falsely identified occurrences of dynamic interaction identified in the absent simulations was higher than expected (e.g., 98 of 1000 simulations at the 100% sampling resolution; Figure 2).

< Approximate Location of Figure 2 >

The Cs index also was successful at identifying correctly the presence of dynamic interaction in all of the simulated scenarios (Figure 2). However, Cs was highly susceptible to Type I error, which was more severe than Don in that Cs identified 380 of 1000 absent cases as having significant dynamic interaction at the 100% sampling resolution, down to 222 of 1000 significant cases at the coarsest resolution (Figure 2). However, raw Cs index values were

relatively consistent across sampling resolutions, which suggests Cs, as an index, may be useful without the formal statistical testing through the calculation of p -values.

The Lixn statistic performed poorest of all eight indices in that it was highly susceptible to both Type I and Type II errors (Figure 2). Lixn failed to correctly identify dynamic interactions in many of the present scenarios (Type II error), but this problem tended to be reduced at finer sampling resolutions (e.g., 736/100 correctly identified as present at the 100% sampling resolution vs. only 83/1000 at the 10% sampling resolution – Figure 2). More problematic is the fact that Lixn also produces a high level of Type I errors; between 262 and 380 of 1000 of the absent scenarios were identified as having significant dynamic interaction. The rate of Type I error also appears to increase at finer sampling resolutions, making the use of Lixn problematic with modern high-resolution telemetry systems (e.g., GPS collars). The raw Lixn values appear to be robust to changes in sampling resolution, but are hindered by high variability in output results (and overlap of index distributions between present and absent scenarios) leading to confusion in quantitative assessments (e.g., p -values).

As a path-based index of cohesive movement, Cr appears to be robust to changes in sampling resolution (Figure 2). DI, on the other hand, was more sensitive to changes in sampling resolution than Cr; lower DI values occurred at finer sampling resolutions (Figure 2). However, DI may be easier to interpret because of a relatively low variation in output values, and accurate assignment to dynamic interaction when one actually is present (conversely, no dynamic interaction for absent cases). Thus, at the global analysis level, it appears both Cr and DI provide relatively robust and similar results.

To further examine simulation results, we explored the relationship between index values and the proportion of time spent in the interactive phase (P_{int}) in present scenarios and level of

static interaction (AOP) in absent scenarios, focusing on the 100% sampling resolution. Several patterns emerged from the correlation analysis (Figure 3; top row). Prox, Ca, Cs, HAI, Cr, and DI all showed a strong, positive relationship with P_{int} ($r \geq 0.6$; Figure 3). Lixn on the other hand showed a very weak positive relationship with P_{int} ($r = 0.209$; Figure 3). Further, by plotting significant vs. non-significant results, we can see that with Lixn, Type II error occurred across the range of P_{int} scenarios suggesting that Lixn produces misleading interpretations even when substantial interaction is present. The correlations associated with Don were ignored because we only were able to plot p-values, which are not meaningful in this context.

< Approximate location Figure 3 >

In the absent scenarios, all indices showed a relatively weak relationship (Figure 3; bottom row) with the level of static interaction (AOP) in the scenario (ignoring Don, since we can only plot p -values). With those indices not employing statistical tests (Prox, Ca, HAI, Cr, DI), index values were near 0 in all cases, correctly identifying no interaction. For Don, Lixn, and Cs, Type I errors were produced across the range of AOP values (Figure 3), which is problematic because it infers that a range of static interaction levels can result in misleading interpretations.

We take one pair of dyads from the simulation to examine, in finer detail, the nature in dynamic interaction, and the presence of Type I & II error. In the present case, the proportion of time in the interactive phase was 0.53, and predictably, the level of static interaction was also higher in the present case (AOP = 0.75) than in the absent case (0.30) (see the Supplementary Material). First, looking at the dyad with interaction present, we see that Prox, Ca, and HAI provide consistent results across all sampling resolutions (Table 4). Cr and DI both show substantial interaction is present, but as seen before, the values are influenced by sampling

resolutions, increasing with coarser sampling data (Table 4). Cs and Don both successfully identify significant interaction at all scales, while Lixn identifies significant interaction only at the 100% and 33% resolutions (Table 4). In the absent scenario, Prox, Ca, HAI, Cr, and DI, all identify no interaction in the data, each index ~ 0 . Don and Lixn, correctly identify the absence of interaction; however, Cs incorrectly identifies significant interaction at all five scales (Type I error – Table 4).

< Approximate location Table 4 >

To demonstrate how varying phases of dynamic interaction occur throughout simulated trajectories, we plotted time series of di (along with proximity) to graphically investigate the temporal phases of interactive behaviour of the two simulated dyads (Figure 4). Based on the simulation parameters (see Supplementary Material) we know that the proportion of time in the interactive phase was $P_{int} = 0.53$, which occurred across multiple phases. From the localized time-series graphs, we identify when (and for how long) interactive behaviour occurs. In the absent scenario, we see several instances later in the trajectories where the two objects become proximal, but throughout the level of di remains near 0, correctly identifying no interactive behaviour.

< Approximate location Figure 4 >

4.2 – Empirical Data: White-tailed Deer

Based on computed indices of static interaction (AOP) we predict little dynamic interaction in dyad 1 (AOP = 0.17), but greater dynamic interaction in dyads 2 and 3 (AOP = 0.67 and 0.57, respectively). For dyad 1, 3 of the 8 indices indicated dynamic interaction in at least one sampling resolution (i.e., either 30 min or 6 hr), but no interaction at the coarsest sampling interval (24 hour) for all eight indices (Table 5). In general, indices did not show a

strong or consistent indication that these two individual deer were exhibiting dynamic interaction. Also, for this particular dyad, indication of dynamic interaction appeared to disappear as sampling resolution became coarser when using Don, Cs, and Lixn; otherwise, indices did not reveal any interaction.

< Approximate location of Table 5 >

In dyad 2, the results showed much conflicting interpretation of whether dynamic interaction was present at the different sampling resolutions and with each index (Table 5). The Don and Cs indices identified significant attraction at all three sampling resolutions, Lixn indicated random use, and Prox, Ca, HAI, Cr and DI showed the absence of any dynamic interaction behaviour (Table 5). However, as Cr is similar to interpreting correlations, the values (from 0.095-0.16) might be interpreted as minimal correlation in movements. Thus, in dyad 2, it is particularly difficult to conclude whether or not dynamic interaction exists, which underscores the difficulty in selecting an appropriate index.

With dyad 3, results indicated substantial and consistent dynamic interaction among seven of the indices and at each sampling resolution (Table 5). Lixn suggested that there was random use of the shared area across the three sampling resolutions. Given the ubiquitous identification of dynamic interaction by 7 of the 8 indices, at all three sampling resolutions, we conclude that positive interactive behaviour (i.e., both attraction and cohesive movement) does exist in dyad 3.

While DI provides an overall index of cohesive movement, the local index di can be used to examine spatial and temporal variations in cohesive movement behaviour. Due to varying levels of dynamic interaction among the 3 dyads of deer, we plotted time series of di (and temporal patterns of proximity between the two deer in meters) to graphically investigate the

spatial and temporal patterns of: 1) no interaction (top plot; dyad 1), 2) infrequent or minimal interaction (middle plot; dyad 2), and 3) strong dynamic interaction (bottom plot; dyad 3) (Figure 4). In the plot of dyad 1, we first observe that distance between this dyad never exceeds 800 m. However, the observed separation between the dyad appears random because there is little variation in the plot of d_i (minimal variation around $d_i = 0$). In the plot for dyad 2, most simultaneous locations were within 1000 m of each other; however, in a few instances, locations of the two deer were >3000 m apart. Global statistics for the 8 indices revealed discrepancies in the dynamic interaction behaviour in dyad 2. However, plotting d_i revealed that dyad 2 did in fact exhibit dynamic interaction on multiple occasions. Finally, the plot for dyad 3 revealed definitively the presence of strong dynamic interaction. Across much of the 3-month sampling period, the dyad of male deer remained proximal for extended periods of time, with corresponding cohesive movement. Although dynamic interaction is occurring across most of the sampling period, this graph reveals periods of variable levels of dynamic interaction through time.

< Approximate location Figure 4 >

5 – Discussion

The simulated data (and subsequent analysis) allowed the identification of several indices that will be useful when applied to empirical wildlife telemetry data; including high resolution data such as those collected from GPS collars. The case study on white-tailed deer revealed that minimal AOP resulted in minimal dynamic interaction, but higher levels of AOP did not necessarily equate to dynamic interaction behaviour because AOP relies on a 2-dimensional home range that does not account for the simultaneous use of these areas, which is inferred using both point- and path-based measures of interaction. The results from all eight indices

corroborated what is known about the seasonal biology of white-tailed deer; dyad 3 was a dyad of male deer of ~3 years of age that were part of the same bachelor group. Although we used white-tailed deer as a case study to assess various indices of dynamic interaction and behaviour; the indices and guidelines we discuss can be applied much more broadly to animal behaviour studies, and even for the analysis of any two moving objects in space and time (e.g., dyads of vehicles, cell-phone users, athletes, etc.).

5.1 – Comparison across indices

The Prox, Ca, and HAI indices produce nearly identical values in all cases, owing to the similarity in their derivation. In our examples, HAI produced similar values to Prox and Ca and identical interpretation of attraction in both the simulation study, and in the white-tailed deer case study. Our results also suggest that three of the classical indices of dynamic interaction (Don, Cs, and Lixn) can be misleading, especially with high-resolution telemetry data. Misleading results are due to statistical testing procedures being especially susceptible to Type I error. Type II error was only problematic in the case of Lixn, as Don and Cs were only not-significant in those present scenarios where interaction was low ($P_{int} < 0.2$; Figure 3). Plots and contingency tables accompanying the Don statistic may be more useful for interpretation than computed p -values; for instance, when examining the effect of the d_c parameter. Similarly, the Cs index may still be a useful measure of dynamic interaction (despite the high type I error rate when used in a hypothesis testing framework) because it was able to adequately separate between the presence and absence of dynamic interaction. In the simulation experiment, Cs showed a direct relationship with the proportion of time spent in the interactive phase. Further, Cs measures a unique property of the data apart from other indices by utilizing the raw distances between fixes rather than a subjectively defined distance threshold (d_c). Unlike the other indices,

Lixn index tests for dynamic interaction based on simultaneous use of the shared area (Minta, 1992). However, despite examining co-occurrence of the shared area, Lixn appears to be poorly suited for measuring dynamic interaction in wildlife telemetry datasets.

Cr and DI measure dynamic interaction as the cohesiveness in movement using a path-based approach. Cr values were consistent across sampling intervals, making it a suitable candidate for measuring dynamic interaction with modern telemetry datasets. The primary limitation of Cr is that it is dependent on measuring correlations relative to a mean path vector, which is typically not meaningful in the context of dynamic interaction analysis. DI was sensitive to changes in sampling resolution producing a lower index value at the highest resolution. The advantage of the DI approach is in examining spatial variation in dynamic interactions through the local level statistic – di.

5.2 – Static vs. dynamic interaction

We looked at three white-tailed deer dyads containing static interaction levels of AOP = 0.17, 0.67, and 0.57, respectively. However, only dyad 3 (AOP = 0.57) showed substantial dynamic interaction, which agrees with the seasonal biology of male deer during this time; male deer form bachelor groups during spring and summer (Hirth 1977). Thus, we were able to identify a dyad of deer belonging to the same bachelor group using dynamic interaction metrics, particularly di (see Figure 4). Further, while the converse may be true (i.e., no static interaction implies no dynamic interaction), our analysis suggests that the relationship between the level of static interaction and presence of dynamic interaction is complex and inferring dynamic interaction from static interaction can be misleading. For example, with our simulations, we produced a range of AOP values, from which no interaction was present. Incorrect inferences may be most problematic for species inhabiting relatively large home range areas, where joint

space use (i.e., home range overlap) can occur without individuals ever encountering one another from a temporal standpoint. Quantitative indices of dynamic interaction allow researchers to examine a wide range of questions relating to animal behaviour and general ecology, and go beyond typical measures of static interaction (e.g., home range overlap). Current methods (e.g., those outlined here) only begin to scratch the surface of the potential for space-time analysis in wildlife systems where multiple animals are tracked simultaneously with high resolution tracking devices.

Recent research has suggested that measures of static interaction (like AOP) can be used to estimate contact-rates and levels of dynamic interaction between wildlife, important in modeling disease transmission (Robert, Garant & Pelletier 2012). Our analysis reveals the flaws in this assumption, as even moderate levels of static interaction may have highly variable contact rates and levels of dynamic interaction (e.g., Figure 3). However, some disease transmission occurs via mechanisms that simply relate to spatial overlap, through feces or saliva (e.g., chronic wasting disease, Williams *et al.* 2002), or intermediate hosts (e.g., West Nile virus, Marra *et al.* 2004). Thus, the nature of disease transmission will be important in identifying whether measures of static or dynamic interaction are appropriate.

5.3 – Scale

Our simulation study outlined a key problem commonly encountered in wildlife movement analysis; inferences made at one scale of analysis do not necessarily hold at other scales (see Laube & Purves 2011 for a more thorough discussion of this). Indices that do not formally test statistical significance appear to be less sensitive to varying scales (i.e., Prox, Ca, HAI, Cr, DI) when compared to indices that implement statistical tests (i.e., Don, Cs, Lixn). Beyond scale, inference among indices is impacted by the nature or level of dynamic interaction

present. Most methods appear to successfully identify strong dynamic interaction when present (e.g., simulations, and deer dyad 3) with greater inconsistencies occurring for infrequent or low levels of dynamic interaction (e.g., deer dyad 2). Our guidelines will help inform the selection of appropriate indices given varying scales and levels of dynamic interaction.

The implementation of the local-level statistic (i.e., d_i), along with time-series plots of proximity (e.g., in Figure 4 and Figure 5), reveals information on infrequent (e.g., deer dyad 1), variable (e.g., deer dyad 2), and frequent (e.g., deer dyad 3) interactions. The prevalence of infrequent and variable interactions in wildlife is unknown, which typically is the motivating factor for assessing the level of dynamic interaction, and the d_i index represents a new metric for revealing both frequent and infrequent interactive behaviour. Animals are now routinely tracked for an extended duration (e.g., several months) with fine resolution telemetry fix rates (e.g., sub-hour sampling intervals), allowing the identification of rare and periodic interactive behaviour, which has important implications on a wide range of studies such as disease spread (Böhm *et al.* 2008), patterns of sociality (Gorman *et al.* 2006), and predator-prey dynamics (Eriksen *et al.* 2008).

We only superficially examine the temporal local dynamics in d_i . More sophisticated analysis could involve other temporal variables to investigate more complex problems, such as circadian rhythms, seasonality, and weather factors. Variations in the level of dynamic interaction (measured through d_i) may be a result of different behaviour states that can relate to resting, foraging, or travelling behaviour (Dzialak *et al.* *Unpublished data*). Including a quantitative characterization of movement behaviour (e.g., Morales *et al.* 2004; Jonsen, Flemming, & Myers 2005; Gurarie, Andrews, & Laidre 2009) for comparison could enhance interpretation of changes in dynamic interaction when using the d_i measure. Similarly, by

mapping the local statistic d_i , one can investigate the role of fine scale landscape and environmental variables on the observed patterns of dynamic interaction. For example, in northern Alberta, Canada, high levels of anthropogenic disturbance are causing increased permeability in the landscape, resulting in a higher potential for caribou predation by wolves (Latham *et al.* 2011). To assist in maintaining the caribou population, the Government of Alberta has promoted the culling of wolves. Novel dynamic interaction analysis, through local d_i , could help reveal the landscape characteristics (e.g., habitat, fragmentation, topography) associated with predation in order to better inform land management policies (e.g., Dzialak *et al.* 2011; Wasser *et al.* 2011), rather than adopt more extreme measures such as culling.

5.4 – Statistical testing

In wildlife telemetry research, the effects of sampling resolution and autocorrelation are well documented (e.g., home range delineation – Swihart & Slade 1985; Seaman & Powell 1996, habitat selection models – Otis & White 1999; Nielsen *et al.* 2002, behaviour analyses – Boyce *et al.* 2010). Yet, little is known about the effects of autocorrelated data and sampling resolution on indices of dynamic interaction. Serial autocorrelation in successive fixes of telemetry data increases with higher sampling frequency (Dray, Royer-Carenzi & Calenge 2010) and hinders the use of methods where independence is assumed (Swihart & Slade 1985), as standard errors will typically be underestimated. In the presence of highly autocorrelated data, statistical tests can be overly sensitive, producing false positives more frequently as the degree of autocorrelation increases. While some have argued that the autocorrelation problem can be overcome by down-sampling telemetry data until it is functionally independent (Swihart & Slade 1997), this procedure has been criticized due to loss of biologically relevant data (de Solla, Bonduriansky & Brooks 1999). Alternately, it may be more effective to implement statistical

597 methods that accommodate (de Solla *et al.* 1999; Nielsen *et al.* 2002), are less sensitive to
598 autocorrelated structures (Fieberg 2007), or adjust the null distribution so that it is appropriate
599 for autocorrelated data (White & Harris 1994). With dynamic interaction analysis, it is pragmatic
600 to think of the autocorrelation problem from a sampling strategy perspective, that is, more
601 (autocorrelated) data provides a better representation of the animals true movement path (Fieberg
602 2007). Finer space-time analysis is possible with greater sampling resolution, enabling better
603 estimates of true dynamic interaction and contact rates between individuals.

604 Several of the indices we examined use formal statistical tests for the presence of
605 dynamic interaction that require the generation of null distributions in order to test the
606 expectation of no interaction. In Don and Cs, these null distributions are generated by permuting
607 the observed fixes of the two animals and measuring the distance between the two permuted
608 fixes. Generating null distributions through permutations of observed data assumes that the data
609 are independent and identically distributed within individual trajectories, but also that the two
610 individuals move independently of one another. As such, permutations typically result in an
611 incorrect expectation leading to increased Type I error when data are autocorrelated (White &
612 Harris 1994). Further, Cs is more susceptible to Type I errors than Don, owing to the use of raw
613 distance values in its calculations. More appropriate methods for generating null expectations for
614 statistical tests are warranted, either using random walk simulations (e.g., White & Harris 1994;
615 Miller 2012) or by developing more appropriate mechanistic models.

616 With Lixn the statistical test is based on expectations derived from the relative area
617 values of each home range overlap section (inhabited by α only, β only, and overlapping area).
618 We initially thought that if the area of home range overlap is relatively large, Lixn is susceptible
619 to Type I error; conversely, if the overlap is relatively small, Lixn may be susceptible to Type II

error. However, from the simulation study, we revealed that Lixn was susceptible to Type I error across a range of overlap values (Figure 3). Given that Lixn relies explicitly on the calculation of individual home ranges, Lixn is further confounded by problems associated with producing reliable home range estimates (e.g., Hemson *et al.* 2005; Börger *et al.* 2006; Downs & Horner 2008). Thus, Lixn represents a measure of simultaneous home range use, somewhere in between typical measures of static interaction (like AOP) and the other measures of dynamic interaction. Animals typically use their home range in a non-homogenous fashion (Samuel, Pierce & Garton 1985); therefore expectations derived from the overlap of home ranges may be misleading relative to actual space use intensity patterns – typically represented by a utilization distribution (Worton 1989). An improved formulation for Lixn could derive the expected values as a function of the joint distribution of two individual utilization distributions (see Powell 2000; Fieberg & Kochanny 2005), assuming the animals move independently of one another.

5.5 – Guidelines

The role of classical hypothesis testing in ecological analysis continues to be questioned (e.g., Hobbs & Hilborn 2006), and in the context of measuring dynamic interactions, our results suggest that procedures avoiding null hypothesis testing provide greater insight into interactive behaviour patterns. Most times, statistical hypothesis testing is not the goal; rather it is the identification of an ecological mechanism (e.g., why are animals interactive at a given point?). The usefulness of Prox, Ca, and HAI owe to the simplicity of their (near identical) calculation and interpretation, and as demonstrated produce nearly identical results. The Don and Cs indices suffer from the susceptibility of their statistical testing procedures to Type I errors, and in the case of Cs, a problem magnified with high resolution GPS telemetry data. Cs, due its formulation based on raw distances, may still be useful to examine this separate property of the data;

however, we suggest that a subjective interpretation be employed. The Don index measures attraction similar to Prox, Ca, and HAI, and we advocate the use of those methods over the Don index. The Lixn index suffers from the same statistical problems as Don and Cs, but also from the configurational problems related to the general task of home range delineation. Lixn performed poorly when viewed as a stand-alone index and provided contrasting results in the white-tailed deer case study, and as such we do not recommend its use.

Novel path-based measures of dynamic interaction (i.e., Cr, DI) examine the cohesiveness in movement segments, rather than proximity or arrangement of fixes represented as spatial points. Of these two metrics, Cr appeared to be least sensitive to sampling resolution, but did suffer from high variation in index values. DI provides novel insight into the spatial variation in dynamic interaction behaviour through the use of the local di statistic. Thus, di is most useful with high resolution GPS telemetry data because of the ability to examine spatial and temporal changes in dynamic interaction behaviour. Neither Cr or DI consider the spatial distance between individuals, and analyzing dyads alongside some measure of proximity (e.g., Figure 4) provides added context for these path-based measures of dynamic interaction.

The following points can be used to guide decisions when studying dynamic interaction in wildlife telemetry datasets. First, it is necessary to identify the presence of temporal overlap in α and β to assess if a dyad offers potential for interactive behaviour. A measure of static interaction (e.g., AOP, as used here) can be used to assess joint space use. Second, Prox, Ca, or HAI can be used as an index of attraction or avoidance behaviour. Alternatively, Cs can be used as a measure of attraction or avoidance that is based on raw distances; however statistical inference should be avoided. Third, Cr or DI can be used as an index of the overall level of

cohesion in movement segments. Finally, d_i can be used to further investigate local-level variations in the cohesiveness of movement, especially within proximal episodes.

5.6 – Future Directions

The development of more sophisticated simulation models that emulate the complex nature of dynamic interactions present in wildlife dyads is required to further advance understanding of the capability of current and future methods aimed at measuring dynamic interaction behaviour. Here we provide a simple and straightforward procedure for simulating the presence of dynamic interaction in movement dyads using biased correlated random walks (Codling *et al.* 2004), where the bias component is set to be the current location of the other individual. We vary parameters related to distance-decay between individuals and bias-strength over ranges that have been tested in studies looking at correlated random walks biased towards favorable habitat patches (e.g., Barton *et al.* 2009; Fronhofer *et al.* 2013). Further testing is required to examine the role of these parameters in the context of interactive behaviour.

Agent-based models (Bennett & Tang 2006) offer the opportunity to incorporate increasingly detailed and sophisticated interactive behaviour patterns into simulations. New technologies are now integrating robotic agents into real-world scenarios that are capable of interacting with live organisms (Krause, Winfield & Deneubourg 2011). Programming different movement patterns with robotic agents may provide novel opportunities to study new and unique problems looking at different interactive behaviour in robot-organism dyads.

Researchers are now capable of directly measuring animal contacts through the use of proximity collars. Proximity collars utilize ultra-high frequency radio (UHF) to detect when two (or more) collars are within a pre-programmed distance of another (Prange *et al.* 2006). Specifically, proximity collars measure contact rates directly, as opposed to inferring contact as

is done with telemetry data through the use of the temporal threshold t_c and measures such as Prox. This direct measurement of contact is especially important in the study of disease transmission, where existing tracking systems are hindered by the lack of information between fixes (Böhm, Hutchings & White 2009). Traditional tracking technologies also have been limited in studying dynamic interactions and contact rates in smaller animals due to the combined effect of their fine-scale movements and the positional error of VHF or GPS sensors. Also, missing telemetry fixes are often prevalent due to the cryptic habitats frequented by smaller animals (e.g., nests, burrows, and man-made structures) further motivating the use of alternative sensors. For example, interesting social behaviour has been revealed in possums (Ji, White & Clout 2005) and raccoons (Prange, Gehrt & Hauver 2011) using proximity collars. Proximity collars are limited in that they provide no location information on where contacts occur, but can be analyzed with temporal variables, or additional bio-sensors (e.g., Laske, Garshelis, & Iaizzo 2011), to study timing patterns and rates of contacts. A combined tracking-proximity collar system would be advantageous in order to simultaneously investigate contacts along with location (Davis *et al.* 2013) and to provide validation data for tracking-based dynamic interaction indices.

The future of dynamic interaction research likely lies with modifying more complex mechanistic movement models (e.g., Morales *et al.* 2004; Jonsen *et al.* 2005) for studying interactive behaviour patterns. Given the flexible inferential framework under which most of these models are developed (see Patterson *et al.* 2008), incorporating the effects of mobile con- or cross-specifics in order to study dynamic interactions is imperative to further advancing mechanistic movement models (Haydon *et al.* 2008; McClintock *et al.* 2012). For example, in studying grey seals, McClintock *et al.* (2012) utilize a small number of known ‘centres of attraction’ in order to model seal movements. Extension of a similar model to the study of

dynamic interactions might assume, for example, that during an interactive phase, centers of attraction would be the locations of another individual based on biased random walks, as in our simulation study. In predator-prey situations, this relationship would be further complicated by the attraction of predators to prey, and the avoidance of prey to predators. As they are able to explicitly accommodate environmental covariates (e.g., Patterson *et al.* 2009), mechanistic movement models are primed to take dynamic interaction analysis to the next phase, whereby the combined effect of habitat and other environmental covariates on dynamic interaction is explicit within the analysis framework.

6 – Conclusion

There still is much to be learned about animal behaviour. Despite recent technological advances, much research builds on early studies that relied on visual observations of animals (Hirth 1977), which is limited by animal activity patterns, habitat use, and observation bias. For example, early accounts on the breeding behaviour of white-tailed deer were based on visual observations, but recent molecular genetic techniques have revealed greater insight into the breeding biology of deer (e.g., DeYoung *et al.* 2009). Then, indices of dynamic interaction can be leveraged to further study rare behavioural interactions that are not readily observed visually while in the field. Other avenues of research that may benefit from recently developed techniques to study dynamic interactions and contact rates (e.g., contact at d_c) include: studies of behaviour and ecology, territory defense, determining mating and reproduction events, assessing disease spread through direct contact, interspecific competition for resources, and intra- and interspecific interactions. One of the most pervasive topics deals with potential for disease spread, particularly when wild animal species come into contact with domestic livestock

(Wyckoff *et al.* 2009). Combining behavioural indices with spatially-explicit landscape data or genetic data will provide greater insight into unobservable phenomena that shape animal populations (demographics and dynamics) and long-term fitness measures (e.g., reproductive success).

In summary, the calculation of contact rates and measures of dynamic interaction offer promise in studying dynamically moving objects in a wide range of fields from pure scientific discovery and ethology to application and management. Herein, we have provided general points on the formulation, interpretation, and use of dynamic interaction indices that can be used to guide future research. Specifically, we have found existing techniques relying on significant-tests to be misleading (e.g., Don, Cs, and Lixn) due largely to the propensity to falsely identify dynamic interaction when it is absent. Further, local-level analysis provides more illuminating evidence of the complex nature of interactive behaviour in wildlife dyads; especially with modern high-resolution telemetry systems. In future research, it will prove useful to combine local-level measurements of dynamic interaction (e.g., di, Long & Nelson 2013) with landscape data to determine where interactions are linked to; for example, to determine preferred resources on the landscape, dietary or niche overlap (within and between species), and the potential for disease spread. To make these methods and indices as widely available as possible, we have implemented each of the eight indices in the R statistical computing environment, and made this code openly available to other users <Website Link>.

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Table 1: Selected examples of applications involving the study of dynamic interactions using wildlife telemetry data.

Index	Species	Data	Study Objective	Citation
Prox	white-tailed deer (<i>Odocoileus virginianus</i>)	VHF	Parturition	(Bertrand <i>et al.</i> 1996)
	maned wolves (<i>Chrysocyon brachyurus</i>)	GPS	Familial bonds	(Bandeira de Melo <i>et al.</i> 2007)
Ca	maned wolves (<i>Chrysocyon brachyurus</i>)	VHF	Inter- & intra-sex behaviour	(de Almeida Jácomo <i>et al.</i> 2009)
	red wolves (<i>Canis rufus</i>)	GPS	Sociality, group behaviour	(Karlin & Chadwick 2011)
Don	wood mice (<i>Apodemus sylvaticus</i>)	VHF	Mating	(Tew & Macdonald 1994)
	raccoons (<i>Procyon lotor</i>)	VHF	Philopatry	(Gehrt & Fritzell 1998)
	coyote (<i>Canis latrans</i>)	VHF	Inter- & intra-sex behaviour	(Chamberlain, Lovell & Leopold 2000)
	badgers (<i>Meles meles</i>)	VHF	Sociality, group behaviour	(Böhm <i>et al.</i> 2008)
Cs	lynx (<i>Lynx canadensis</i>)	VHF	Inter- & intra-sex behaviour	(Poole 1995)
	red & grey squirrels (<i>Sciurus vulgaris</i> & <i>carolinensis</i>)	VHF	Interspecific	(Kenward & Hodder 1998)
	wolves & moose (<i>Canis lupus</i> & <i>Alces alces</i>)	GPS	Interspecific	(Eriksen <i>et al.</i> 2008)
Lixn	badgers (<i>Taxidea taxus</i>)	VHF	Inter- & intra-sex behaviour	(Minta 1993)
	grizzly bear (<i>Ursus arctos</i>)	VHF	Inter- & intra-sex behaviour	(Mace & Waller 1997)
	mountain lion (<i>Puma concolor</i>)	VHF	Familial bonds	(Nicholson <i>et al.</i> 2011)
HAI	coyote (<i>Canis latrans</i>)	VHF	Management and control	(Bromley & Gese 2001)
	coyote (<i>Canis latrans</i>)	VHF	Habitat relations	(Atwood & Weeks 2003)
Cr	caribou (<i>Rangifer tarandus</i>)	VHF	Sociality, group behaviour	(Shirabe 2006)
DI	grizzly bear (<i>Ursus arctos</i>)	GPS	Mating	(Long & Nelson 2013)

Table 2: Eight indices of dynamic interaction for wildlife telemetry data. Refer to Table 3 for terminology. In all indices, except for Lixn, simultaneous fixes ($T_{a\beta}$) are determined using a temporal threshold (t_c) and d_c is a threshold distance for proximal fixes ($S_{a\beta}$).

Index	Reference	Sig. Test	Data	Tests	Interpretation
Prox	-	-	Point	Ratio of $ST_{a\beta}$ fixes to $T_{a\beta}$ fixes, based on d_c .	Prox can be interpreted much like Ca (see below) and is similarly based on d_c .
Ca	Cole (1949)	-	Point	The proportion of all fixes that are $ST_{a\beta}$ based on d_c .	Ca ~ 1 – attraction Ca ~ 0 – no association
Don	Doncaster (1990)	χ^2 test	Point	If the distribution of distances of $T_{a\beta}$ is different than the distances of permutations of all fixes.	Based on the contingency table and a χ^2 test looks for significant attraction in $ST_{a\beta}$ for a given d_c .
Lixn	Minta (1992)	χ^2 test	Point	The simultaneity of usage of the shared area of each home range.	$L_{ixn} > 0$, shared use is simultaneous (attraction) $L_{ixn} < 0$, shared use is solitary (avoidance) $L_{ixn} \sim 0$ shared use is random
Cs	Kenward (1993)	Wilcoxon signed-rank test	Point	For differences between distances of $T_{a\beta}$ and distances of permutations of all fixes.	Cs ~ 1 – attraction Cs ~ -1 – avoidance
HAI	Atwood & Weeks (2003)	-	Point	Number of $ST_{a\beta}$ fixes within the shared area of the home range against solitary use of shared area.	HAI ~ 1 – attraction HAI ~ 0 – avoidance
Cr	Shirabe (2006)	-	Path	Correlation of movement segments tested against respective path means. Identical to Pearson correlation statistic (r).	Cr ~ 1 – positive correlation (cohesion) Cr ~ -1 – negative correlation (opposition) Cr ~ 0 – no correlation (random)
DI	Long & Nelson (2013)	-	Path	Cohesion in individual movement segments (global and local), with respect to distance and direction.	DI ~ 1 – cohesive movement DI ~ -1 – opposing movement DI ~ 0 – random movement

Table 3: Terminology and notation used for describing telemetry data and dynamic interaction methods.

Term	Explanation
α or β	Individuals of a dyad (telemetry data)
dyad	Pair of individuals (α and β)
fix	A telemetry record (spatial location and time stamp)
t_c	Time threshold
d_c	Distance threshold
$T_{\alpha\beta}$	Temporally simultaneous fixes based on t_c
$S_{\alpha\beta}$	Spatially proximal fixes based on d_c
$ST_{\alpha\beta}$	Spatially proximal and temporally simultaneous fixes based on d_c and t_c
v_t, w_t	Movement segment, vector connecting two consecutive fixes
\bar{v}, \bar{w}	Mean movement segment for an entire path

Table 4: Index results from single scenario analysis in the simulation experiment, * denotes significant values ($p < 0.01$). A video, along with the parameterization, of these two dyads is available in the supplementary material.

		Prox	Ca	Don		Lixn		Cs		HAI	Cr	DI
Present	<i>100%</i>	0.427	0.427	0	*	0.626	*	0.607	*	0.456	0.324	0.277
	<i>50%</i>	0.427	0.427	0	*	0.586		0.608	*	0.452	0.364	0.287
	<i>33%</i>	0.435	0.435	0	*	0.765	*	0.609	*	0.458	0.359	0.305
	<i>20%</i>	0.413	0.413	0	*	0.343		0.608	*	0.432	0.409	0.332
	<i>10%</i>	0.427	0.427	0	*	-0.738		0.607	*	0.446	0.401	0.387
Absent	<i>100%</i>	0	0	0.262		-0.614		0.051	*	0	0.012	-0.002
	<i>50%</i>	0	0	0.582		-0.614		0.051	*	0	0.016	-0.001
	<i>33%</i>	0	0	0.791		-0.593		0.050	*	0	0.010	0.005
	<i>20%</i>	0	0	1		-0.538		0.051	*	0	-0.022	-0.010
	<i>10%</i>	0	0	1		-0.497		0.051	*	0	0.001	-0.016

Table 5: Results of dynamic interactions using empirical GPS data collected from white-tailed deer in Oklahoma, USA. Dynamic interactions were tested at three temporal resolutions (30 min, 6 hr, and 24 hr) for eight indices of dynamic interaction. Values highlighted in grey indicate significance at $p < 0.01$.

Dyad	Sampling Resolution			Interpretation
	30 min	6 hr	24 hr	
1				
Prox	0.017	0.030	0.018	No proximity
Ca	0.014	0.025	0.016	No attraction
Don (p-val.)	0	0.0042	0.66	Varies depending on scale, attraction at 30 min and 6hr
Cs	0.013	0.02	0.01	Varies depending on scale, attraction at 30 min and 6 hr
Lixn	-0.19	0.11	0.058	Simultaneous use of shared area at 30 min, but not at coarser scales
HAI	0.037	0.053	0.044	No attraction within shared area
Cr	-0.022	0.079	0.060	No correlation
DI	-0.004	0.021	-0.014	No dynamic interaction
2				
Prox	0.071	0.073	0.072	No proximity
Ca	0.069	0.07	0.07	No attraction
Don (p-val.)	0	0	0	Attraction
Cs	0.10	0.10	0.10	Attraction
Lixn	0.37	0.31	0.32	Random use of shared area
HAI	0.074	0.077	0.075	No attraction within shared area
Cr	0.095	0.16	0.11	Very low positive correlation
DI	0.029	0.11	0.028	No dynamic interaction
3				
Prox	0.57	0.57	0.58	Poximity
Ca	0.53	0.52	0.54	Attraction
Don (p-val.)	0	0	0	Attraction
Cs	0.40	0.39	0.36	Attraction
Lixn	0.11	0.21	0.21	Random use of shared area
HAI	0.60	0.60	0.61	Attraction within shared area
Cr	0.59	0.66	0.72	Positive correlation
DI	0.28	0.57	0.61	Positive dynamic interaction (cohesive movement)

Figure 1: Empirical GPS telemetry data for three white-tailed deer dyads ($n = 6$ deer). Contours (grey and black polygons) represent 95% volume contour home ranges using kernel density estimates, along with static interaction measured as the area of overlap proportion (AOP) of the two individual home ranges. AOP is depicted as the grey shaded region. Deer in dyads 1 and 3 were tracked for approximately 3 months; while in dyad 2, deer were tracked approximately 6 months.

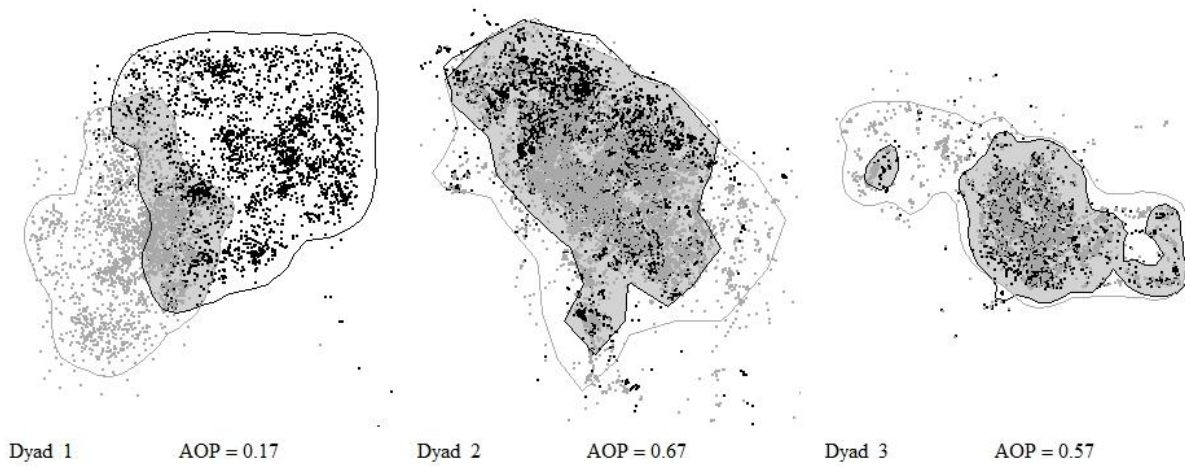


Figure 2: Results from simulations where 1000 scenarios were generated, each containing one dyad, under two circumstances: 1) dynamic interaction present (medium grey histogram) and 2) dynamic interaction absent (light grey histogram). Dark grey indicates where the index values overlap. Each scenario was examined at five sampling resolutions (100% , 50%, 33%, 20%, 10% of fixes). Along with the histogram of index values, we present the mean, standard deviation (in brackets), and number of significant results where appropriate ($p < 0.01$ – denoted by *). Note: values plotted for Don are simply p -values as no stand-alone index is generated with Don.

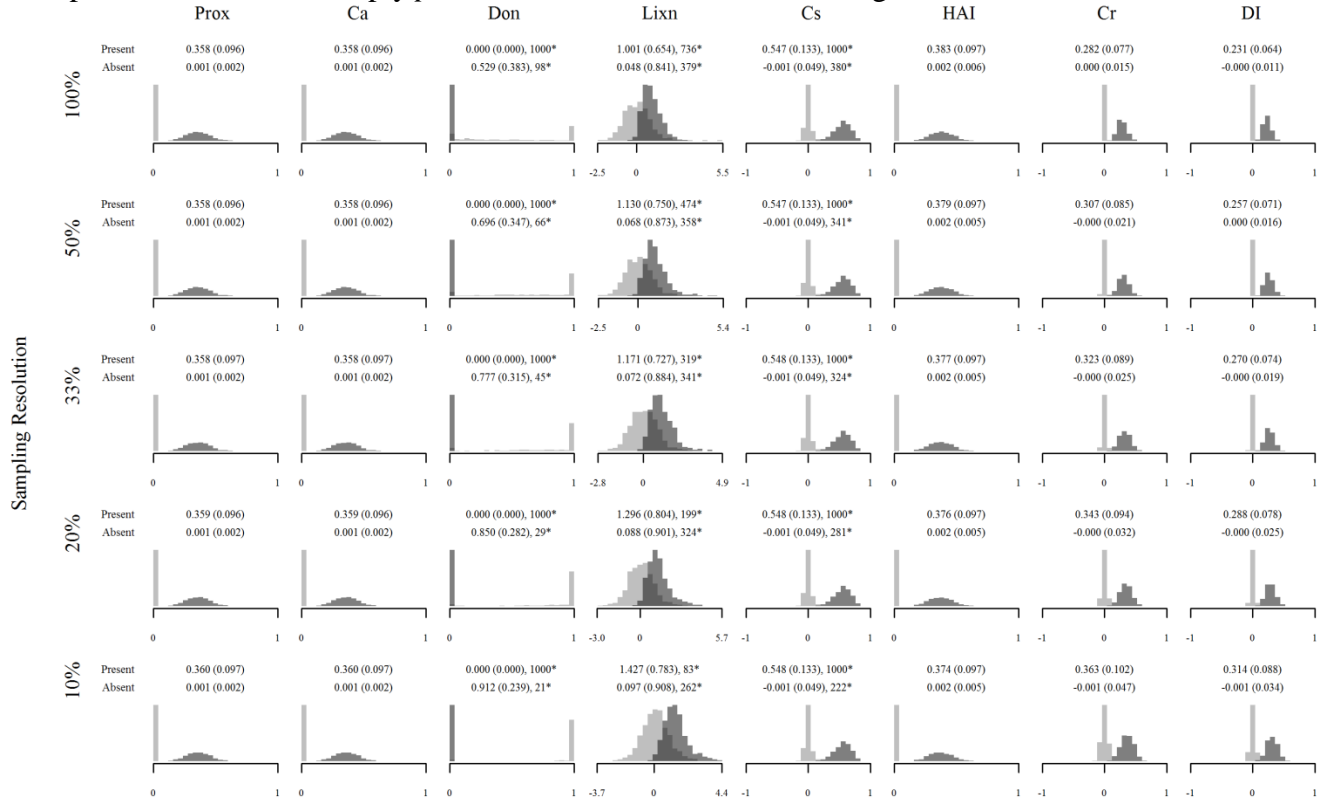


Figure 3: Correlation between indices of dynamic interaction and proportion of time in the interactive phase (Pint) from the scenarios where interaction was simulated as present (top row); and static interaction (AOP) from the dyads where interaction was simulated as absent (bottom row). Values plotted using an open circle denote Type II error in the top row (no significant interaction when present) and Type I error in the bottom row (significant interaction when absent).

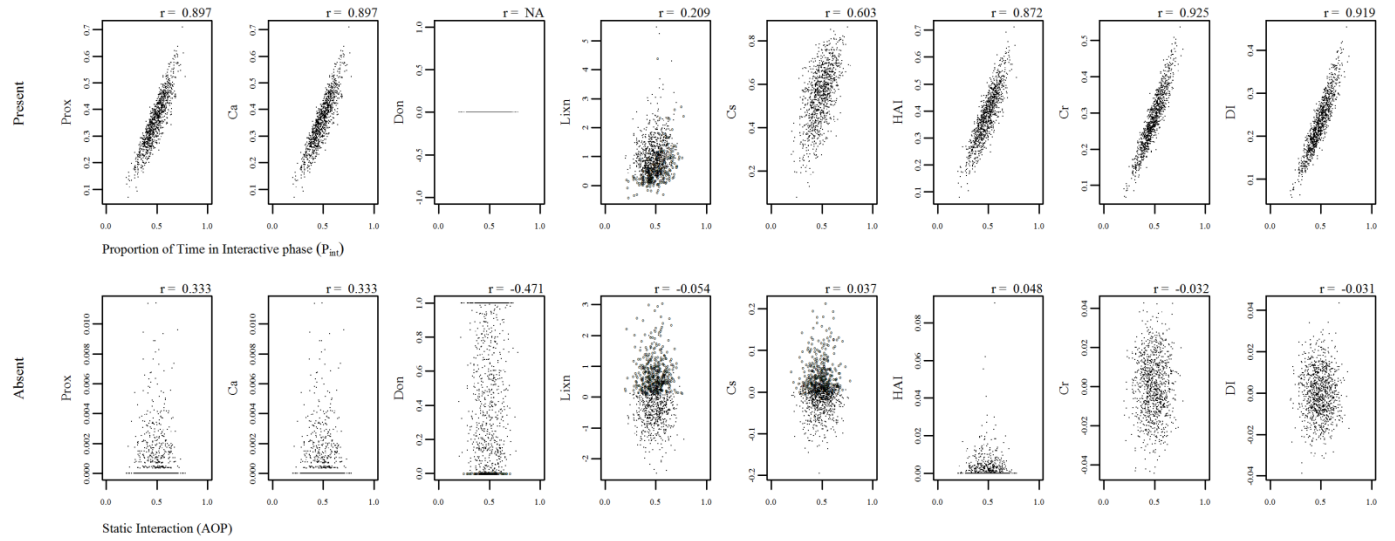


Figure 4: Time series plot of the local d_i statistic (in black; developed by Long and Nelson 2013) and proximity (meters; in grey) for the 100% sampling resolution from a single pair of dyads from the simulation study (see Supplementary Material A), one with interaction absent (top) and one with interaction present (bottom). The black dotted line represents random interaction at $d_i=0$, whereas the grey dotted line represents the critical threshold for identifying proximal fixes ($d_c = 50$ m).

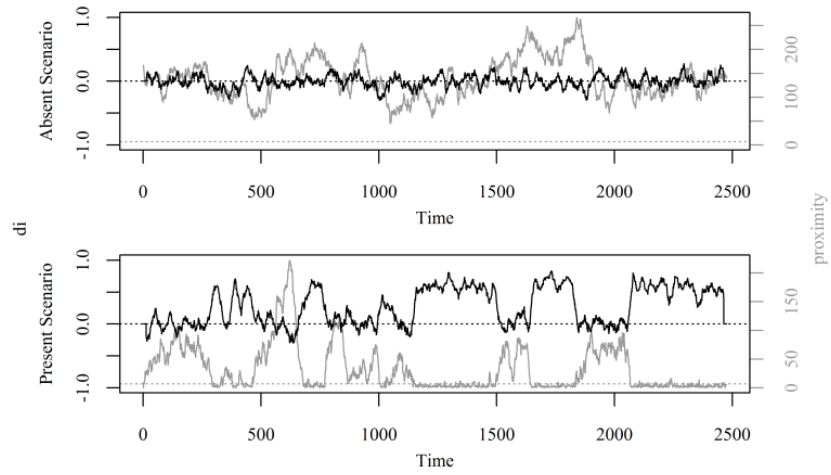
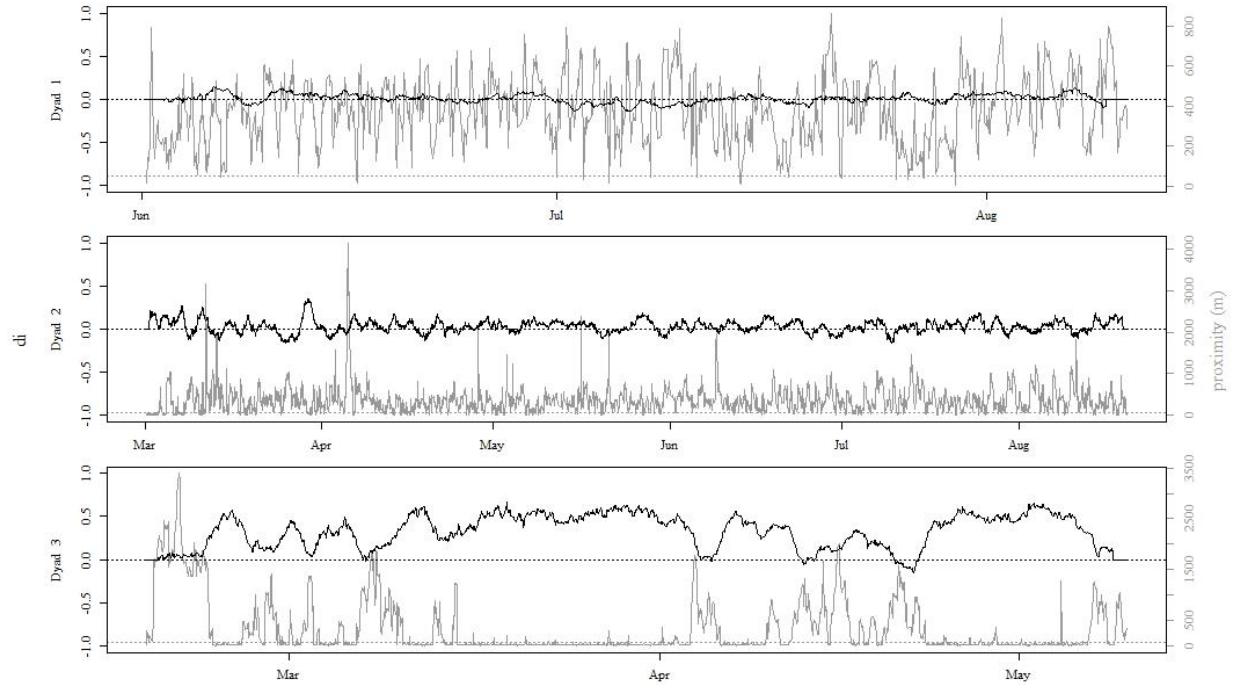


Figure 5: Time series plot of the local d_i statistic (in black; developed by Long and Nelson 2013) and proximity (meters; in grey) for the 30 min sampling interval for three white-tailed deer dyads ($n = 6$ deer). A 24 hr moving window average of d_i was used to minimize noise. The index d_i is presented on y-axis 1 and proximity (m) on y-axis 2. The black dotted line represents random interaction at $d_i=0$, whereas the grey dotted line represents the critical threshold for identifying proximal fixes ($d_c = 50$ m).



Supplementary Material:

1. Figure showing two simulated dyads along with 95% kernel home range estimates; a) interaction present, b) interaction absent. These two scenarios were used for finer treatment of dynamic interaction in the simulation study. The parameters used were:

$$n = 2475$$

$$h = 3.46$$

$$r = 0.19$$

$$p = 0.004$$

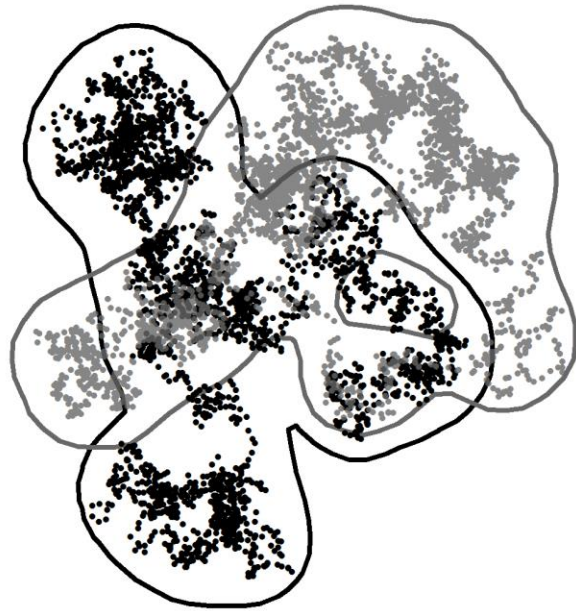
$$b = 3.9$$

$$\rho = 0.87$$

This resulted in a $P_{int} = 0.53$ for the present case (a) with an AOP = 0.75 and in the absent case (b) AOP = 0.30.



a) Interaction Present



b) Interaction Absent

2. R Code (function) for producing the biased correlated random walk (BCRW) used to simulate the presence of dynamic interaction.

< Attach R code as file for uploading >